
NEW SPECIES OF BRITTLE STARS FROM THE WESTERN ATLANTIC, *OPHIONEREIS VITTATA*, *AMPHIOPLUS SEPULTUS*, AND *OPHIOSTIGMA SIVA*, AND THE DESIGNATION OF A NEOTYPE FOR *OPHIOSTIGMA ISOCANTHUM* (SAY) (ECHINODERMATA: OPHIUROIDEA)

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ABSTRACT. *Ophionereis vittata*, new species, heretofore misidentified as *O. reticulata* (Say) or *O. olivacea* H.L. Clark, occurs from Florida and the Caribbean at depths from 23 to 126 m. *Ophiostigma siva*, new species, which is fissiparous and usually six-armed, was previously considered to be conspecific with five-armed *Ophiostigma isocanthum* (Say). The latter species is redescribed and a neotype designated. *Ophiostigma siva* and *O. isocanthum* are sympatric, ranging from Bermuda to the Caribbean, from the intertidal to depths over 40 m. *Amphioplus sepultus*, new species, has been reported to be the most common intertidal amphiurid in southern Florida and is known only from Floridian waters. *Amphioplus abditus* (Verrill), into which *A. sepultus* was formerly placed, is distributed from Maine to Georgia.

INTRODUCTION

This is an account of three species of brittle stars that are widespread in warm waters of the western Atlantic and consistently have been mistaken for sympatric congeners. Of one, *Ophionereis vittata*, few individuals have been found, possibly because it belongs to the relatively inaccessible "deep-reef fauna" (Hendler and Miller, 1984; Hendler and Peck, 1988). In contrast, *Amphioplus sepultus* is "the most common intertidal amphiurid of South Florida" (Thomas, 1962:654, as *Amphioplus abditus* (Verrill)). Similarly, *Ophiostigma siva* can occur in profusion, with over 100 individuals per liter of algal substratum (Hendler and Littman, 1986, as *Ophiostigma isocanthum*).

In this contribution the five-armed species *Ophiostigma isocanthum* (Say), sister species of the fissiparous, six-armed *O. siva*, is redescribed. A neotype is designated because Say's (1825) original specimen is lost. The present contribution includes diagnoses, full descriptions, and lists of designated type material for the three new taxa. However, abridged descriptions and color illustrations of these species are provided in Hendler et al. (1995).

The following abbreviations for institutions and programs are used in this paper: BLM (United States

Bureau of Land Management), IRCZM (Indian River Coastal Zone Museum, Harbor Branch Oceanographic Institution), LACM (Natural History Museum of Los Angeles County), LMRS (South Atlantic Outer Continental Shelf Area Living Marine Resources Study), MCZ (Museum of Comparative Zoology, Harvard University), MMS (United States Minerals Management Service), SOFLA (Southwest Florida Shelf Ecosystem Study), UMML (Rosenstiel School of Marine and Atmospheric Sciences, University of Miami), USNM (National Museum of Natural History, Smithsonian Institution), and UZM (University Zoological Museum, Copenhagen).

SYSTEMATIC ACCOUNT

Family Ophionereididae

Genus *Ophionereis* Lütken, 1859

Ophionereis vittata, new species

Figure 1A–C

Ophionereis reticulata: Lyman, 1878:224 (not *Ophiura* [= *Ophionereis*] *reticulata* Say, 1825), author notes "Station 11, 37 fathoms, 1 specimen," corresponding to MCZ 1603, which is *Ophionereis vittata*; 1883:253 (not *Ophiura* [= *Ophionereis*] *reticulata* Say, 1825, in part), author notes "Station 278, Barbados, 69 fathoms," corresponding to USNM 6430, which is *O. vittata*.

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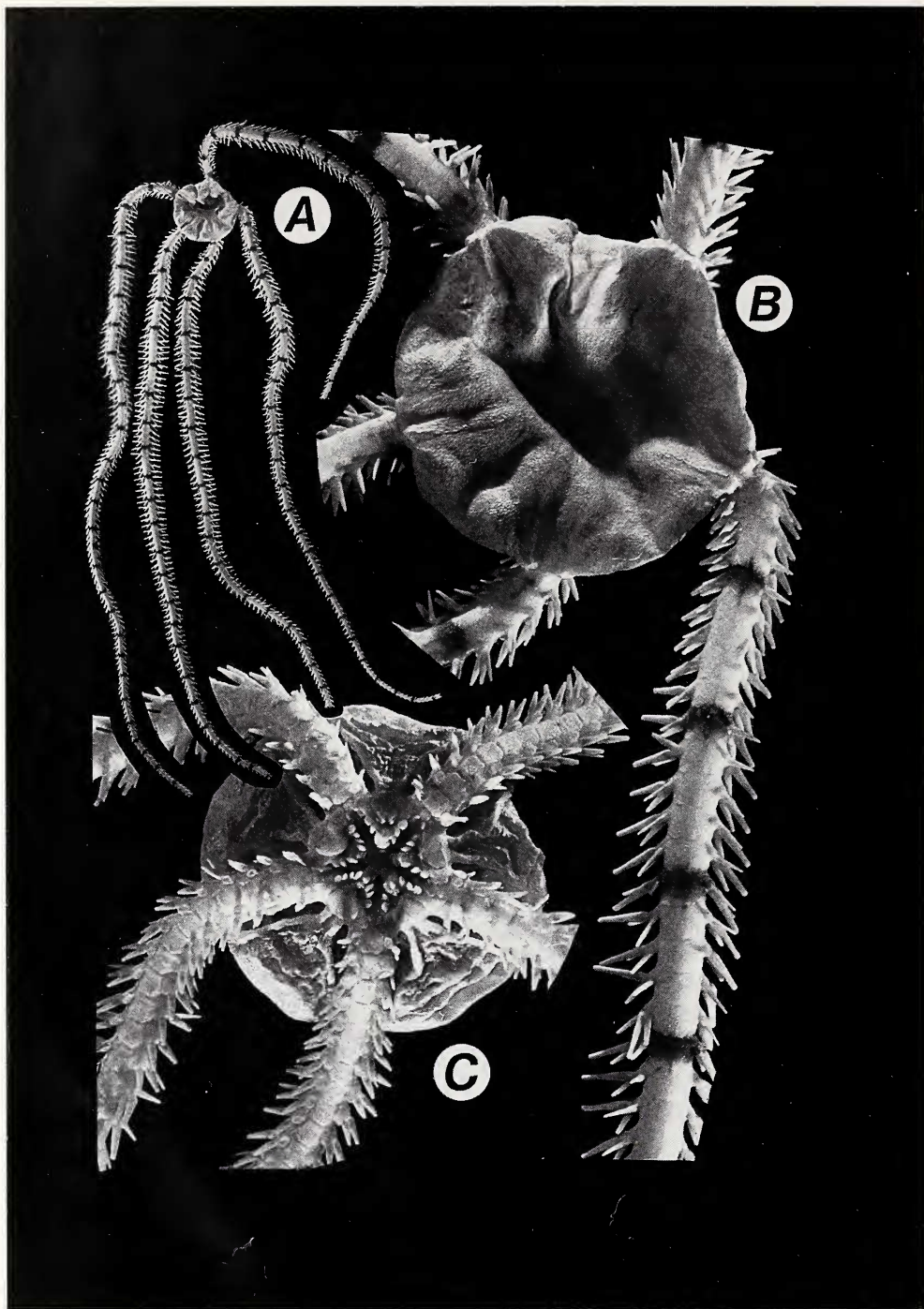


Figure 1. *Ophionereis vittata*, new species, holotype LACM 83-134.2: A, entire, dorsal view; B, disk, dorsal view; C, disk, ventral view. Disk diameter = 7.0 mm.

Ophionereis olivacea: Thomas, 1973:590–593, fig. 3 (not *Ophionereis olivacea* H.L. Clark, 1901, in part).

Ophionereis sp.: Hendler and Peck, 1988:413.

This species, first collected by the R/V *Blake* during the 19th century, was misidentified as *Ophionereis reticulata* (Say) by Lyman (see synonymy above). Thomas (1973:592) mistakenly regarded it

as *O. olivacea* H.L. Clark and mentioned that Clark's description of *O. olivacea* "... is accompanied by a singularly poor illustration." Indeed, most of Clark's description could apply to either *O. olivacea* or *O. vittata*. However, Clark specified that *O. olivacea* is marked by "color above olive green, spotted on the disk with yellow; arms banded with a darker shade of green ... outside of oral shield is a patch of dark brown, as in *reticulata*." This corresponds to the situation in the specimen of *O. olivacea* (MCZ 4250) collected, identified, and discussed by Clark (1918). However it does not apply to *O. vittata*, which lacks the dark brown patch that is characteristic of *O. olivacea*. Furthermore, *O. vittata* invariably possesses "golden reticulation" (Thomas, 1973:593) on an otherwise grayish disk. Moreover, Clark (1901:248) mentioned the presence of more than one pair of accessory dorsal arm plates on the "first few joints" of *O. olivacea*, whereas *O. vittata*, as illustrated by Thomas (1973:592), has "... accessory plates often appearing to be composed of overlapping scales (Fig. 3A)" on much of its arm.

ETYMOLOGY. *Vittata*, feminine form of the Latin adjective meaning "decorated with ribbon," in reference to the colorful stripe, bands, and network pattern adorning living individuals.

MATERIAL EXAMINED. Unless otherwise stated, all specimens from Belize were collected using scuba gear and the ichthyocide "Noxfish," ESE of Carrie Bow Cay on the seaward slope of the Belize Barrier Reef, 16°48.14'N, 88°04.50'W, by G. Hendler with the assistance of divers noted in the Acknowledgments. Designated types originally cataloged as *O. vittata* unless otherwise noted.

Holotype. BELIZE: (LACM 83-134.2), holotype, dry, Sta. Belize 83 No. 10, 7 Nov. 1983, 80 ft.

Paratypes. FLORIDA, ATLANTIC: (LACM 85-275.2), 1 alc, Sta. LK 55a, 17 Aug. 1985, 24°32.0'N, 81°24.3'W, Looe Key National Marine Sanctuary, 24-26 m, scuba, coll. G. Hendler et al. GULF OF MEXICO, OFF FLORIDA: (USNM E12182), originally as *O. olivacea*, 3 alc, VF Middle Grounds Cr., Sta. 6, 19 May 1973, 28°27'N, 84°19'W, coll. F.J.S. Maturo, 120 ft; (USNM E32313), originally as *O. olivacea*, 1 alc, MMS/BLM SOFLA Sta. 23 II-23-c-TDS, 1 Aug. 1981, 25°16'53"N, 83°37'47"W, off Florida, Gulf of Mexico, 70 m; (USNM E32314), originally as *O. olivacea*, 4 alc, MMS/BLM SOFLA Sta. 23 II-23-a-TDS, 1 Aug. 1981, 25°16'53"N, 83°37'47"W, off Florida, Gulf of Mexico, 70 m. BELIZE: (LACM 83-134.3), 2 alc, Sta. Belize 83 No. 10, 7 Nov. 1983, 80 ft, coll. G. Hendler; (LACM 83-131.3), 1 alc, Sta. CBC 83-9, 6 Nov. 1983, 80 ft; (LACM 85-461.1), 1 alc, Sta. CBC 85-6, 15 Jun. 1985, 75 ft, coll. G. Hendler.

Other Material Examined. FLORIDA, ATLANTIC: UML cat. no. 41.172, 1 alc. GULF OF MEXICO, OFF FLORIDA: MCZ cat. no. 1603, 1 dry; USNM cat. nos. E31841, 1 alc; E31842, 1 alc; E31843, 1 alc; E32312, 1 alc; E32316, 1 alc; E32317, 2 alc; E32318, 1 dry; E32319, 1 alc. BARBADOS: USNM cat. no. 6430, 1 dry. THE GRENADINES: BEQUIA: LACM cat. no. 69-149.1, 1 alc. U. S. VIRGIN ISLANDS: UML cat. no. 41.236, 1 alc. BELIZE: LACM cat. no. 83-132.4, 1 alc. PANAMA: LACM cat. nos. 66-318.1, 1 dry; 66-320.1, 2 alc; USNM cat. nos. E45510, 1 alc; E45509, 1 dry.

DIAGNOSIS. Disk of living individuals adorned with yellow reticulation, arms dorsally with medial red stripe and greenish brown bands. Disk scales small, delicate; primary plates not discernable; genital papillae absent. Oral shield subcordate, nearly equal in length and width. Arms long, slender throughout; joints bear 3 compressed arm spines; middle spine longest, equal in length to the width of a joint, tip slightly expanded, surface microscopically roughened. One or more supplementary scales distal to most accessory dorsal arm plates. Superficial ossicles thin and delicate; arm spines and tentacle scales translucent in alcoholic specimens.

DESCRIPTION OF HOLOTYPE. Disk diameter 7.0 mm; length of longest arm 60 mm. Disk rounded pentagonal, somewhat inflated, delicate. Arms long, very slender, narrow at edge of disk, increasing in width to approximately 12th to 15th arm joint, outer 1/3 of arm gradually tapering to filiform tip. Arms gently rounded dorsally, flattened ventrally; dorsal and ventral arm plates of successive joints in contact, lateral arm plates connected by soft tissue. Superficial ossicles delicate, thin; in alcohol, arm spines and tentacle scales appear translucent.

Disk covered with minute, thin, imbricating scales; scales smallest at center of disk, largest near radial shields at periphery of disk; primary plates not discernable; radial shields small, triangular, approximately twice as long as wide.

Each jaw with 1 apical oral papilla, 3 pairs of oral papillae laterally; proximal lateral papillae bluntly pointed, distalmost larger, broader, flattened; tentacle scale arising from first ventral arm plate. Teeth with squared tips, stereom of proximal edge imperforate.

Oral shield subcordate, length and width nearly equal, proximal edge bluntly pointed, distal edge broadly rounded. Madreporite slightly longer than wide, bearing 5 pores. Adoral shield covered proximally by oral shield; radial edges rounded, abutting first ventral arm plate in mouth angle.

Bursal slits long, extending to periphery of disk, bordered by small, thin scales; genital papillae absent. Ventral interbranchial field covered with layer of minute, thin scales.

Dorsal arm plates rounded triangular, longer than wide at base of arm; rounded hexagonal throughout wide central region of arm, only slightly wider than long; markedly longer than wide on distal region of arm. Accessory dorsal arm plates abutting distal half of dorsal arm plate, less than half the plate in length; present from base to tip of arm. Supplementary scales originating at distal edge of accessory dorsal arm plate, one or more scales on each joint; present on proximal 3/4 of arm.

Lateral arm plates slightly flared, bearing 3 erect arm spines. Dorsal and ventral spines laterally compressed, markedly tapering to blunt tip. Dorsal spine shorter and narrower than ventral spine, broader on joints near disk edge than on distal joints. Middle spine longest, dorsoventrally compressed; shaft

tapering toward center, tip expanded; edges of spines thin, microscopically rough. Length of middle spine equal to width of arm joint in broad central region of arm. Spines near arm tip slender, acutely pointed.

First ventral arm plate small, subtriangular; second plate wider than long; third plate equidimensional; succeeding plates longer than wide. Plates shield-shaped, with narrow proximal edge convexly rounded, distal edge broad, convex, with medial notch; lateral edges deeply concave alongside tentacle pore.

One tentacle scale covering each pore, large, ovoidal; proximal end narrow, distal end broad.

Coloration. In holotype and other individuals when alive, ground color of disk gray to white, covered with an open network of thin, brilliant yellow to brownish yellow lines extending onto the ventral interradii; arms whitish with a thin medial stripe of red originating between the radial shields, extending to arm tip, every 3–8 joints with a black and dark greenish brown band extending to ventral surface; arm spines whitish with basal band of yellow, orange-brown, or brown. Dorsal arm plates may be tinged with red, ventral arm plates with yellow or brown, lateral arm plates with yellow, red, or brown; oral shields, adoral shields, and jaws may be blotched with yellow, orange, or brown. Protracted tube feet, equal in length to the arm joint, are transparent or whitish translucent. The color of the ripe gonads is visible through the ventral body wall; testes are white, ovaries are pinkish red.

In alcoholic or dried specimens, pigmentation lost except for the black and green bands and for short sections of the arm stripe that become green or brown; in some instances, a dusky or brown portion of the netted pattern remains on the disk.

VARIATIONS. Disk diameters of available material range from 2.9 to 9.5 mm; arm length ranges from 23 to 89 mm; the ratio of arm length/disk diameter ranges from approximately 7 to 13. The smallest specimen (LACM 85-275.2) differs from others examined in having dorsal arm plates longer than wide and having middle arm spines of a length less than the width of the arm segment. Differences between some of the paratypes and the holotype include adoral shields with proximal tips meeting above the oral shield, teeth with proximal tip pointed or irregular in shape, middle arm spine with the shaft very slightly to markedly narrowed before the tip, and madreporite with more (or less) than 5 pores.

COMPARISONS. The association of supplementary scales with the accessory dorsal arm plates places *O. vittata* among the *Ophionereis* species referred to *Ophiocrasis* H.L. Clark, 1911. The group, according to A.M. Clark (1953), includes *Ophionereis dubia* (Müller and Troschel), with which she unites *Ophiocrasis dictydisca* H.L. Clark and *Ophiocrasis marktanneri* Matsumoto and possibly *Ophionereis squamulosa* Koehler. Supplementary scales are also present in *Ophionereis oli-*

vacea H.L. Clark and *Ophionereis perplexa* Ziesenhenné (Hendler, pers. obs.).

Ophionereis vittata is distinguished from congeners by its unique pattern of arm stripe and bands and its absence of a dark patch distal to the oral shield. In contrast to *O. squamulosa* and *O. olivacea*, it lacks oral papillae. Unlike *O. dolabriformis* and *O. perplexa*, its arm spines do not exceed the length of an arm joint, and they are delicate and translucent instead of dense. Its arms are relatively longer than those of *O. dubia*, which attain a length only 7–8 times the diameter of the disk, and the dorsal arm plates of the latter species are subtriangular rather than hexagonal as in *O. vittata*.

DISTRIBUTION. The range of *O. vittata* encompasses the perimeter of the Caribbean Region and extends into the Gulf of Mexico. However, sizeable gaps separate the collecting sites: the Greater and Lesser Antilles, Panama, Belize, and Florida. In addition to the localities noted above, the species has been photographed at Cayman Brac (by E. Fish, Divers Alert Network 1991 Calendar). Although one specimen from St. John was reportedly collected from shallow water (Thomas, 1973), others originated at depths between 23 and 126 m.

BIOLOGY. This species occupies hard-bottom habitats near the edge of the continental shelf. This zone has been referred to as the “mixed region” of the Caribbean (Lyman, 1869:309) and its inhabitants characterized as the “deep-reef fauna” (Hendler and Peck, 1988). In recent years, newly described ophiuroids have been reported from this habitat, which starts near the lower limits of conventional scuba activity and extends to depths sampled with submersibles (Hendler and Miller, 1984; Hendler and Turner, 1987; Hendler, 1988; Hendler and Peck, 1988).

Near the upper limit of its bathymetric range, on the Belize Barrier Reef, *O. vittata* was collected on the forereef slope near massive shelves of *Montastrea annularis* (Ellis and Solander), large flat agariciids, and other stony corals, in areas with a significant cover of *Halimeda* spp., sponges, and gorgonians. Individuals were cryptic and encountered when ichthyocide was applied to drive invertebrates from the reef. On the intermediate-deep reef off Looe Key, Florida, an individual was found within a clump of *Halimeda* algae. Individuals from deeper water off Panama and Colombia were dredged from hard bottoms characterized by coral plates, coralline lumps, and shell fragments.

Several *Ophionereis vittata* were collected at the same stations as *O. reticulata* and *O. olivacea* in Panama and Belize; however, *O. reticulata* is typically found in shallow-water reef habitats and *O. olivacea* in mangrove algae, seagrass beds, and less commonly on the forereef slope (Hendler et al., 1995).

Gonads are visible through the thin ventral body wall of several specimens; there are 6–12 gonads per interradius, and the sexes are separate. Two females had relatively large gonads, and 10 of the

largest oocytes were measured in each individual. The mean oocyte diameter was 0.20 mm, but these cells may not have been fully ripe. This is considerably smaller than the 0.4-mm oocytes of *Ophioreis olivacea* H.L. Clark, which broods its young (Hendler and Littman, 1986; Byrne, 1991). None of the specimens of *O. vittata* brooded embryos in their bursae. The oocyte diameter of *O. vittata* is slightly smaller than the 0.24-mm oocytes of *O. annulata* (Le Conte) and similar to the 0.20-mm oocytes of *O. squamulosa* Koehler (Hendler, 1982, 1991). All three species have oocyte sizes typical for ophiuroids with abbreviated development, and *O. annulata* and *O. squamulosa* have lecithotrophic larvae (Hendler, 1982, 1991), suggesting that the new species might have a similar mode of development.

Family Amphiuroidae

Genus *Ophiostigma* Lütken, 1856

Ophiostigma isocanthum (Say, 1825)

Figures 2A–C, 4A

Ophiura isocantha Say, 1825:150–151.

Ophiocoma isocantha: Müller and Troschel, 1842: 103.

Ophiostigma moniliforme: Lütken, 1856:13; 1859: 181, 186, 234 (in part).

Ophiostigma isocantha: Lyman, 1860:258.

Ophiostigma isocanthum: Lyman, 1865:12, 103–104, 199, figs. 8, 9 (in part). Ljungman, 1866:317. H.L. Clark, 1901:344. Hendler and Littman, 1986: 33–38 (in part). Hendler and Peck, 1988:413 (in part).

Ophiostigma isacantha: Ljungman, 1871:636, 657. Heilprin, 1888:316. H.L. Clark, 1898:412; 1899: 131.

Ophiostigma isacanthum: Lyman, 1875:5; 1878: 224; 1880:26; Lyman, 1882:165, 311, 314, 324, 380, pl. 42, fig. 16; 1883:229, 254. Rathbun, 1879: 155. Verrill, 1899:377; 1907:325; H.L. Clark, 1901:240, 249, 262 (in part); 1915:244; 1919:56, 58; 1933:36, 50–51 (in part); 1942:377 (in part). A.H. Clark, 1922:210. Koehler, 1907:298; 1913: 352, 363–367, pl. 20, figs. 6, 7 (in part); 1914:2, 38, 154, 171 (in part). A.H. Clark, 1921:42; 1922: 210; 1939:446; 1954:377. Nielsen, 1932:308–309. Pearson, 1937:71. Engel, 1939:4, 8. Fontaine, 1953:199, 201. A.M. Clark, 1955:38. Tabb and Manning, 1961:566. McNulty et al., 1962a:229. Thomas, 1962:689–692, fig. 23a, b (in part). Parslow and A.M. Clark, 1963:37, 44. Lewis, 1965: 1074. O’Gower and Wacasey, 1967:210. Tommasi, 1970:40–41. Singletary, 1971:940. Carrera, 1974:iii, 69–71, pl. 5, fig. 2a, b (in part). Alvarez Larrauri, 1981:33. Abreu Pérez, 1983:2. Emson et al., 1985:87–100 (in part). Aronson and Harms, 1985:1483.

This was among the first brittle star species to be described by an American scientist. The initial ac-

count (Say, 1825) was based on a single specimen collected from the Florida Keys. The types of several species published coincidentally with *Ophiura* (*Ophiostigma*) *isocantha* are deposited at the Academy of Natural Sciences of Philadelphia (Spamer and Bogan, 1992), but the Academy has no record of a holotype of *O. isocantha* (E.E. Spamer, pers. comm.). Neither is there a record of the original specimen at The British Museum (Natural History) (G.L.J. Paterson, pers. comm.) to which Say sent some material before his departure, around 1828, for the utopian colony of New Harmony, Indiana (Spamer, pers. comm.). Other potential repositories, the USNM and MCZ, do not hold the type (Downey, 1969).

Say’s description is sufficient to distinguish *O. isocanthum* from any other shallow-water West Indian brittle star. Since the 19th century, there has been a clear concept of Say’s species, and specimens have been illustrated several times (see synonymy). However, as discussed below for *Ophiostigma siva*, authors occasionally have remarked on six-armed individuals in collections of five-armed *O. isocanthum*, either considering them variants or fissiparously reproducing individuals. Formal recognition of the fissiparous individuals as a distinct taxon in the present publication necessitates the redescription of *O. isocanthum* and the designation of a neotype. In accordance with the International Code of Zoological Nomenclature (ICZN) Article 75, the specimen selected as the neotype originated from the Florida Keys, the original collecting locality.

ETYMOLOGY. The original spelling *isocantha* should have been written *isacantha*, but as it is not “demonstrably incorrect” with regard to ICZN Article 32, it must be retained.

MATERIAL EXAMINED. Neotype. FLORIDA, ATLANTIC: (LACM 85-265.3), alc, LK 45, 15 May 1985, 24°33.7’N, 81°25.7’W, Looe Key National Marine Sanctuary, Florida Keys, 11 m, coll. G. Hendler et al.

Other Material Examined. NORTH CAROLINA: USNM cat. nos. E27748, 4 alc; E27749, 5 alc; E27750, 3 alc; E27751, 10 alc; E27752, 2 alc; E28160, 1 alc; E28161, 1 alc; E28162, 2 alc; E28163, 4 alc; E28169, 5 alc; E28170, 6 alc; E28172, 1 alc; E29095, 5 alc; E29096, 2 alc; E29098, 5 alc; E29099, 9 alc; E29100, 1 alc; E29102, 1 alc; E29106, 5 alc; E29107, 3 alc; E29109, 1 alc; E29110, 11 alc; E29111, 1 alc; E29112, 2 alc; E29115, 1 alc; E29116, 1 alc; E29119, 1 alc; E29121, 1 alc; E29122, 29 alc; E29123, 2 alc; E29125, 7 alc; E29126, 9 alc; E29127, 4 alc; E29128, 4 alc; E29130, 3 alc; E29131, 2 alc; E29132, 9 alc; E29133, 1 alc; E29134, 1 alc; E29135, 8 alc; E29136, 29 alc; E29137, 3 alc; E29138, 10 alc; E29139, 4 alc; E29140, 6 alc; E29141, 54 alc; E29142, 3 alc; E29143, 8 alc; E29144, 2 alc; E29146, 2 alc; E29147, 1 alc; E29149, 2 alc; E29150, 12 alc; E29155, 3 alc; E29274, 1 dry; E29275, 3 dry; E29276, 1 dry; E29277, 2 dry; E29417, 7 alc; E30494, 1 alc; E30508, 1 alc; E30524, 1 alc; E32211, 1 alc; E30496, 27 alc; E30525, 1 alc; E33143, 1 alc. GEORGIA: USNM cat. nos. E28165, 1 alc; E28167, 2 alc; E29097, 7 alc; E29101, 9 alc; E29103, 6 alc; E29108, 4 alc; E29113, 1 alc; E29114, 8 alc; E29118, 2 alc; E29120, 1 alc; E29124, 3 alc; E29129, 1 alc; E29151, 1 alc; E29152, 1 alc; E29156, 4 alc; E29157, 1 alc; E29158, 1 alc; E29387, 1 alc; E30242, 19 alc; E30244, 3 alc; E30249, 9 alc. FLOR-

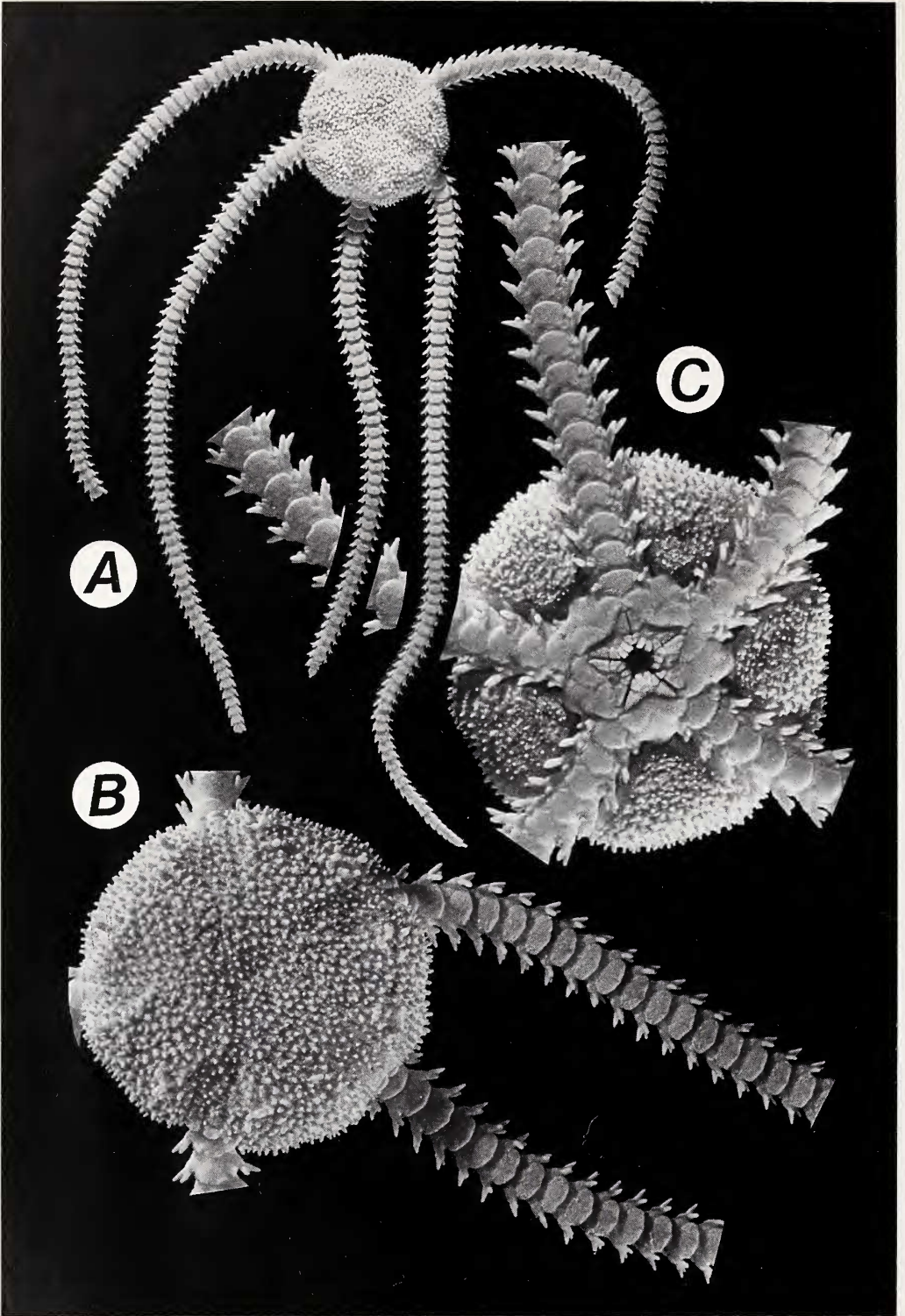


Figure 2. *Ophiostigma isocanthum* (Say), neotype LACM 85-265.3: A, entire, dorsal view; B, disk, dorsal view; C, disk, ventral view. Disk diameter = 6.0 mm.

IDA, ATLANTIC: LACM cat. nos. 70-291.5, 1 dry; 84-230.5, 1 alc; 85-240.5, 1 alc; 85-242.6, 1 alc; 85-262.4, 2 alc; 85-275.4, 2 alc; 85-268.4, 1 alc; 85-277.4, 1 alc; 88-194.5, 1 alc; 88-197.8, 23 alc; USNM cat. nos. E19742, 1 alc; E20290, 1 alc; E20291, 1 alc; E24331, 2 dry; E28158, 3 alc; E28159, 1 alc; E28164, 1 alc; E28166, 1 alc; E28168, 1 alc; E28171, 1 alc; E29148, 2 alc; E37731, 1 alc; IRCZM cat. nos. 74:257, 1 dry; 74:258, 8 alc; 74:354, 2 dry; 74:356, 7 alc; 74:384, 1 alc; 74:546, 3 alc; 74:549, 3 alc. SOUTHWEST FLORIDA, GULF OF MEXICO: LACM cat. nos. 89-237.5, 1 alc; 89-319.2, 2 alc; 89-322.4, 4 alc; 89-323.5, 1 alc; 89-325.1, 1 alc; 89-327.2, 1 alc; 89-329.5, 2 alc; 89-339.3, 1 alc; 89-348.1, 1 alc; 89-350.1, 1 alc; 89-351.3, 1 alc; 89-352.1, 1 alc; 89-358.2, 1 alc; 89-359.2, 1 alc; 89-365.1, 3 alc; 89-371.1, 1 alc; USNM cat. nos. 6440, 1 alc; 12482, 2 dry; 14199, 3 alc; 14207, 1 dry; 14245, 3 alc; 15430, 2 dry; 15455, 1 dry; 33975, 5 alc; 33976, 1 alc; 33977, 1 alc; E22825, 1 dry; E25232, 1 dry; E28634, 1 alc; E31831, 1 alc; E31832, 1 alc; E31833, 2 alc; E31834, 1 alc; E31835, 1 alc; E31836, 1 alc; E31837, 2 alc; E32327, 1 alc; E32328, 3 alc; E32329, 1 alc; E32330, 1 alc; E32331, 1 alc; E32332, 1 alc; E32333, 1 alc; E32334, 1 alc; E32335, 1 alc; E32336, 1 alc; E32337, 1 alc; E32338, 1 alc; E39139, 1 alc; E39140, 1 alc; E39141, 1 dry; E39142, 3 alc; E39143, 1 dry; E39144, 1 alc; E39145, 1 dry; E39146, 1 alc; E39147, 1 dry; E39148, 3 alc; E39149, 2 dry; E39150, 2 alc; E39151, 5 alc; E39152, 1 dry; E39153, 1 alc; E40920, 1 alc; E40947, 2 alc. BAHAMA ISLANDS: LACM cat. no. 88-211.1, 4 alc; USNM cat. nos. E31328, 1 dry; E31330, 1 dry; E31332, 1 dry; E31340, 1 alc. VIRGIN ISLANDS: USNM cat. nos. 26660, 2 dry; E23014, 1 dry. CUBA: USNM cat. nos. 34733, 1 dry; 34734, 1 alc; 34782, 1 dry; E24183, 1 dry. PUERTO RICO: USNM cat. no. E5448, 1 dry. MEXICO: USNM cat. no. E27783, 1 dry. BELIZE: LACM cat. nos. 81-231.2, 1 alc; 82-124.2, 2 alc; 83-214.2, 2 alc; 83-216.1, 1 alc; 83-217.1, 2 alc; 83-219.2, 1 alc; 85-454.1, 1 alc; 85-455.2, 2 alc; 85-455.4, 11 alc; 85-456.1, 9 alc; 86-55.1, 2 alc; 86-55.2, 1 alc; 86-57.1, 1 alc; 86-63.1, 1 alc; 86-65.1, 1 alc; 86-74.1, 1 alc; 86-77.1, 1 alc; 86-78.1, 1 alc; 86-87.1, 1 dry; 86-489.1, 1 alc; USNM cat. no. E29792, 1 alc. COSTA RICA: LACM cat. nos. 86-98.1, 1 alc; 86-143.1, 2 alc; 86-145.1, 3 alc. PANAMA: USNM cat. nos. E24119, 1 dry; E26396, 1 alc; E26405, 3 alc; E26415, 1 dry; E28383, 4 alc; LACM cat. nos. 39-181.2 AHF, 1 dry; 39-221.2 AHF, 1 dry. COLOMBIA: LACM cat. nos. 39-186.2 AHF, 19 dry; 39-187.8 AHF, 7 dry; 39-188.3 AHF, 19 dry. VENEZUELA: LACM cat. nos. 39-195.3 AHF, 1 dry; 39-213.3 AHF, 1 dry. NETHERLANDS ANTILLES: LACM cat. no. 39-191.8 AHF, 9 dry; USNM cat. nos. 15395, 1 dry; E606, 2 alc.

DIAGNOSIS. The species was described by Say (1825:150-151) as follows: “*O. isocantha*. Disk pentagonal, granulated; spines less than half the length of the transverse diameter of the ray.

“Inhabits the coast of Florida.

“Disk with the angles obtusely rounded; surface with numerous elevated tubercles or granulations, which are not crowded; edge not interrupted by the rays: rays on the back with a single series of transversely, angularly oval plates, on each side of which are two very small spine like scales: spines less than half the transverse diameter of the ray in length, unarmed, prominent, equal, placed in three series: mouth very regular, stellate: colour whitish, rays annulate with greenish.

“Diameter of the disk less than $\frac{1}{4}$ of an inch.

“A single specimen was taken by Mr. Peale.

“The granulations of the disk resemble those of *O. crassispina*, but they are somewhat larger in proportion.”

The diagnosis is revised as follows. Arms 5 in number. Disk covered with short tubercles; several tubercles seated at adradial corner of radial shield especially prominent. Dorsal disk scales bumpy, appearing fused together. Three oral papillae, 2 distal pairs thick, operculate, closing the oral slit. Arm spines 3, peglike, slightly dorsoventrally flattened, gradually tapering to blunt tip. Radial shield broad, bearing tubercles; flat, thick plates joined to and equal in width to narrow distal margin. Adoral plates overlap first ventral arm plates, forming continuous ring. Proximal dorsal arm plates ovoid diamond-shaped, twice as wide as long, in contact on proximal third of arm. Lateral arm plate stereom with expanded peripheral trabeculae. Ventral arm plate length equal to width.

DESCRIPTION OF NEOTYPE. Disk diameter 6.0 mm; length of longest arm 28 mm. Disk round in outline, dorsal surface flattened, inflated interradially, bearing short, blunt tubercles above and below. Arm joints below disk narrower than those beyond edge of disk. Arm gradually tapers from edge of disk to tip, dorsal surface rounded, ventral surface relatively flattened, arm tip dorsoventrally flattened; joints set off by constrictions of lateral arm plates. Major ossicles of disk and arms thick, somewhat swollen, opaque.

Body wall pliable, bumpy, scale covered. Scale edges not discernable; many scales with swollen central region, bearing fixed tubercles, most 0.06–0.14 mm tall, half as wide. One or two exceptionally large, peglike tubercles at adradial edge of each radial shield, approximately 0.3 mm tall, 0.16 mm thick. Radial shield broad, length approximately $\frac{1}{8}$ diameter of disk; shields 4–5 times longer than wide, edges not clearly discernable, bearing scattered, minute tubercles. Flat, thick plate borne on distal end of radial shield, equal in width to distal edge of shield. Primary plates not distinguishable.

Infradental papillae paired, blocklike, in contact; middle oral papillae slightly larger than infradental, pyramidal, broad edge facing oral slit; distal oral papilla largest, spanning middle oral papilla to first ventral arm plate, quadrilateral, much longer than wide, long inner edge incised and ridged. Distal 2 pairs of oral papillae of adjacent jaws in contact, sealing oral gap. Teeth chisel-shaped; proximal edge concave, stereom imperforate; gap between tips of opposing ventral teeth wider than gap between dorsal teeth.

Oral shields arrowhead-shaped, nearly as wide as long, with sharply pointed proximal apex, proximal edges markedly concave, lateral edges short, distal edge bluntly rounded. Center of shield depressed. Madreporite of similar shape, slightly larger than oral shield.

Adoral shield quadrilateral, with part of convex adradial edge adjoining incurved side of oral shield, concave radial edge facing mouth. Adoral shields

with inner ends meeting proximal to oral shield, outer ends meeting or nearly meeting distal to first ventral arm plate, shields thereby forming nearly continuous ring around the mouth.

Prominent genital scale bridging oral shield and bursal slit. Bursal slit narrow, spanning approximately $\frac{2}{3}$ length of interradius; slit inconspicuous, obscured by arm.

Dorsal arm plates with markedly thickened distal edge, extending above proximal surface of succeeding plate. Dorsal arm plates in contact on proximal $\frac{1}{3}$ of arm; distal plates separated by lateral arm plates. Proximal dorsal arm plates approximately twice as wide as long, diamond-shaped with rounded corners; distal plates becoming half-moon-shaped, decidedly smaller than lateral arm plates on distal portion of arm.

Lateral arm plates with stereom of expanded peripheral trabeculae, appearing as transparent, microscopic grains. Lateral plates constricted proximally; distal end broadened, forming thick spine-bearing ridge.

Three arm spines, erect, with rounded base, somewhat dorsoventrally flattened, gradually tapering to blunt tip. Dorsal spine longest, shorter than dorsal arm plate.

First ventral arm plate inserted at distal edge of jaw slit, minute, diamond-shaped, surrounded by distal oral papillae and adoral shields. Other ventral arm plates distal to adoral shields, pentagonal; proximal edges meeting at rounded apex, lateral edges concave, distal edge convex. Ventral arm plates on proximal portion of arm overlapping, plate width exceeding length; ventral plates on central portion of arm separated by lateral arm plates, plate width equals length; ventral arm plates becoming triangular in shape with rounded distal edge on flattened tip of arm.

Tentacle scales paired, minute, ovoid, flattened, only partially covering tentacle pore; scale on lateral arm plate slightly smaller than more distal scale on ventral arm plate.

Coloration. In alcohol, residual pigmentation is pale yellow, some lateral arm plates brown above and below arm, some dorsal arm plates with elongate, brown, medial ring. Dark pigmentation produces appearance of irregular bands and discontinuous medial stripe. For a typical individual in life, the disk above is brown, radial shields have a pale distal tip, the oral shields are white, adoral shields are gray and tan, jaws are brown and tan; the arms above are cream and gray with a chainlike dark brown pattern, ventral arm plates are gray with white highlights, and the arm spines are white.

VARIATIONS. Specimens examined have disk diameters from 0.9 to 6.6 mm and arm lengths from 1.7 to 42 mm. Maximum disk diameter/arm length ratio is $1/8$. Primary plates are evident in individuals smaller than 4.0 mm disk diameter but are not discernable in large specimens. The prominent tubercles associated with the radial shields are even more conspicuous in small specimens than in large

ones. Interestingly, the enlarged tubercles are present on disks that are regenerating subsequent to autotomy. Some features that are distinct in adults are less pronounced in small specimens, such as the degree of overlap of dorsal arm plates and the integrity of the ring of adoral shields.

COMPARISONS. See following species account.

DISTRIBUTION. Previously reported from Bermuda, Florida, the Florida Keys, Dry Tortugas, Gulf of Mexico, Belize, Cuba, Jamaica, Puerto Rico, Tortola, St. John, St. Thomas, St. Croix, Anguilla, St. Barthélemy, St. Christopher, Tobago, Curaçao, Aruba, and Brazil, from less than 1 m to 223 m. Specimens from the USNM and LACM collections extend the range to North Carolina, South Carolina, Georgia, the Bahama Islands, Mexico, Costa Rica, Panama, and Venezuela.

BIOLOGY. The species lives on soft-bottom habitats, in sediments with seagrass, amidst rubble, shell, stones, coral, and coralline algae and under sponges. Individuals are cryptic and can conceal themselves beneath a thin layer of sediment. When freshly collected, individuals usually are coated with fine grains of sediment, which appear to adhere to mucus on the disk and arms.

Gonads are present in some individuals as small as 1.0 mm in disk diameter. Several individuals of moderate size were found to have up to 8 ovaries per interradius, up to 76 oocytes per ovary, the oocytes with a mean diameter of 0.15 mm.

Ophiostigma siva, new species

Figures 3A–C, 4B

Ophiostigma moniliforme: Lütken, 1856:13; 1859: 181, 186, 234 (in part).

Ophiostigma isacanthum: Lyman, 1865:12 (here as *Ophiostigma isocanthum*), 103, 199, figs. 8, 9 (not *Ophiura* [= *Ophiostigma*] *isocantha* Say, 1825, in part). H.L. Clark, 1901:240, 249, 262 (not Say, 1825, in part); 1933:36, 50–51 (not Say, 1825, in part); 1942:377 (not Say, 1825, in part). Koehler, 1913:352, 363–367, pl. 20, figs. 6, 7 (not Say, 1825, in part); 1914:2, 38, 154, 171 (not Say, 1825, in part). Thomas, 1962:689–692, fig. 23a, b (not Say, 1825, in part). Parslow and A.M. Clark, 1963:37 [in synonymy of *Ophiocomella ophiactoides* (H.L. Clark) as “(?) *Ophiostigma isacanthum* (pt), H. L. Clark, 1942, p. 377 (six-armed specimen from Bermuda)”. Carrera, 1974: iii, 69–71, pl. 5, fig. 2a, b (in part). Emson et al., 1985:87–100 (not Say, 1825, in part).

Ophiostigma sp. Hotchkiss, 1982:388, 392–393, 406–408, fig. 173a, b.

Ophiostigma isocanthum: Hendler and Littman, 1986:33–38 (not Say, 1825, in part). Hendler and Peck, 1988:413 (not Say, 1825, in part).

Hotchkiss (1982) described a fissiparous specimen as *Ophiostigma* sp. from Belize and suggested that six-armed individuals may be specifically distinct from *O. isocanthum*. Previously, six-armed

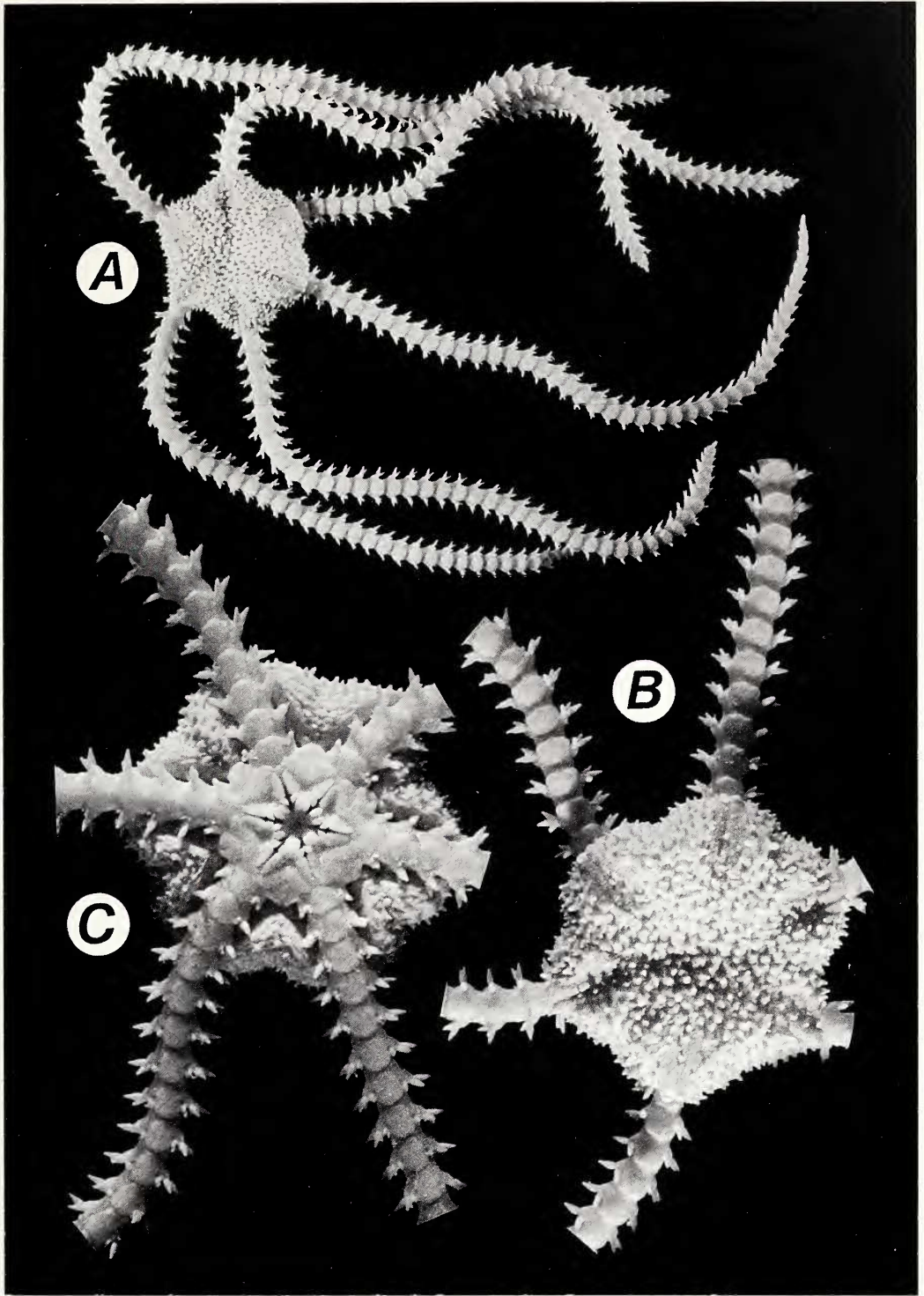


Figure 3. *Ophiostigma siva*, new species, holotype LACM 83-226.1: A, entire, dorsal view; B, disk, dorsal view; C, disk, ventral view. Disk diameter = 4.4 mm.

Ophiostigma were regarded as a variant or as an asexual reproductive stage of the five-armed *O. isocanthum*.

Lütken (1859:234), in discussing five-armed *Ophiostigma moniliforme*, recounted, "Of this species I have had occasion to examine a six-armed specimen, belonging to Apothecary Riise and taken at St. Thomas at a depth of 4 fathoms. The Museum's specimens have only 5 arms." Lütken thought that *O. moniliforme* might be identical to *Ophiura* (= *Ophiostigma*) *isocantha* Say, with which it was synonymized by Lyman (1865) and subsequent authors.

Additional six-armed individuals were reported by H.L. Clark (1901:249), who found that one of four *Ophiostigma* examined from Puerto Rico and one of four from Bermuda had six arms (H.L. Clark, 1942). Koehler (1913, 1914) recorded a six-armed specimen from the Tortugas and another from Key West, Florida. More recent papers have noted that, in Puerto Rico (Carrera, 1974), Jamaica (Emson et al., 1985), and Belize (Hendler and Littman, 1986; Hendler and Peck, 1988), six-armed individuals of "*Ophiostigma isocanthum*" predominate.

H.L. Clark was the first author to suggest that *O. isocanthum* exhibits fissiparity, which he referred to as "autotomous reproduction" (H.L. Clark, 1933:51) and "schizogenesis" (H.L. Clark, 1942:377). The occurrence of fissiparity in *O. isocanthum* was accepted by Thomas (1962:692) but called into question by Parslow and A.M. Clark (1963:37), who suggested that H.L. Clark's (1942) six-armed specimen from Bermuda was a misidentified *Ophiocomella ophiactoides* (H.L. Clark). Parslow and A.M. Clark (1963:38) wrote that "H. L. Clark followed Lütken, Lyman and other nineteenth century workers in assuming that such six-armed ophiuroids are conspecific with the sympatric five-armed forms and represent the juvenile phase of these." In fact, fissiparous *Ophiostigma* are present at Bermuda; Dennis Devaney identified an individual from the island (Pawson, pers. comm.). Six-armed individuals are not a fissiparous growth stage of *O. isocanthum* as suggested by H.L. Clark. Hotchkiss's (1982) proposal that the six-armed *Ophiostigma* represent a separate species is confirmed in the present contribution.

The taxonomic status of fissiparous *Ophiostigma* has been difficult to resolve because five-armed specimens tend to be larger than those with six arms. Therefore specimens of similar size are compared in this study, and since some taxonomic characteristics are altered by the process of fissiparity, caution must be exercised in evaluating affected structures.

ETYMOLOGY. A noun in apposition, from Sanskrit, for the Hindu god of fertility and destruction, in reference to the fissiparous mode of reproduction of this prolific, 6-armed species.

MATERIAL EXAMINED. Designated types originally cataloged as *Ophiostigma isocanthum* unless otherwise noted.

Holotype. BELIZE: (LACM 83-226.1), alc, Sta. CBC 83-14JAN, 16°48.12'N, 88°04.73'W, reef crest, Carrie Bow Cay, Belize, 0.2–1.5 m, coll. G. Hendler.

Paratypes. FLORIDA, ATLANTIC: (LACM 85-242.20), 18 alc, Sta. LK 22, 8 May 1985, 24°32.3'N, 81°24.1'W, Looe Key National Marine Sanctuary, Florida, 6–8 m, scuba, coll. G. Hendler et al.; (LACM 85-275.3), 13 alc, Sta. LK 55, 17 Aug. 1985, 24°32.0'N, 81°24.3'W, Looe Key National Marine Sanctuary, Florida, 24–26 m, scuba, coll. G. Hendler et al.; (LACM 85-277.8), 12 alc, Sta. LK 57, 18 Aug. 1985, 24°31.9'N, 81°25.7'W, Looe Key National Marine Sanctuary, Florida, 24 m, scuba, coll. G. Hendler et al. **BELIZE:** (LACM 81-221.1), 7 alc, Sta. CBC 81-3, 17 Apr. 1981, 16°48.14'N, 88°04.50'W, ESE of Carrie Bow Cay, Belize, 15 m, scuba, coll. G. Hendler; (LACM 83-218.1), 13 alc, Sta. CBC 83-28MAR, 28 Mar. 1983, 16°48.14'N, 88°04.73'W, E of Carrie Bow Cay, Belize, 0–1 m, coll. G. Hendler; (LACM 83-219.1), 41 alc, Sta. CBC 83-31MAR, 31 Mar. 1983, 16°48.12'N, 88°08.73'W, E of Carrie Bow Cay, Belize, 0–1 m, coll. B. Littman; (LACM 83-226.2), 5 alc, CBC 83-14JAN, 16°48.12'N, 88°04.73'W, reef crest, Carrie Bow Cay, Belize, 0.2–1.5 m, coll. G. Hendler; (LACM 85-455.3), 11 alc, Sta. CBC 85-2, 13 Jun. 1985, 16°48.70'N, 88°08.80'W, Blue Ground Range, Barrier Reef Lagoon, Belize, 1 m, coll. G. Hendler; (LACM 86-32.1), 8 alc, Sta. CBC 86-1, 2 Apr. 1986, 16°48.14'N, 88°04.50'W, ESE of Carrie Bow Cay, Belize, 18 m, scuba; (USNM E19910), originally as *O. isacanthum*, 4 alc, Sta. CBC-66A, 29 Apr. 1974, Carrie Bow Cay, Belize, coll. F. Hotchkiss; (USNM E45488), 12 alc, Sta. CBC 81-43, 26 Apr. 1981, 16°48.12'N, 88°04.73'W, E of Carrie Bow Cay, Belize, 0–1 m, coll. G. Hendler; (USNM E45489), 13 alc, Sta. CBC 83-15NOV, 15 Nov. 1983, 16°48.12'N, 88°04.73'W, E of Carrie Bow Cay, Belize, 0–1 m, coll. B. Littman.

Other Material Examined. NORTH CAROLINA: USNM cat. no. E29145, 1 alc. **SOUTH CAROLINA:** USNM cat. nos. E29094, 2 alc; E29104, 1 alc (lot originally included 3 *O. isocanthum*). **FLORIDA, ATLANTIC:** LACM cat. nos. 84-230.13, 2 alc; 85-257.8, 1 alc; 85-262.10, 3 alc; 85-268.13, 6 alc; USNM cat. no. E37724, 3 alc (lot originally included 3 *O. isocanthum*); IRCZM cat. nos. 74:361, 2 dry; 74:412, 1 dry; 74:599, 2 alc (lot originally included 1 *O. isocanthum*). **FLORIDA, GULF OF MEXICO:** LACM cat. nos. 89-237.2, 3 alc; 89-320.3, 1 alc; 89-321.2, 1 alc; 89-323.6, 3 alc; 89-327.3, 1 alc; 89-328.4, 2 alc; 89-329.6, 2 alc; 89-342.4, 3 alc; 89-343.4, 1 alc; 89-347.2, 1 alc; 89-360.2, 1 alc; 89-365.2, 1 alc; 89-366.1, 1 alc; 89-367.5, 1 alc; 89-367.6, 1 alc; 89-376.2, 1 alc; 89-378.3, 4 alc; USNM cat. nos. 14115, 1 dry (lot originally included 3 *O. isocanthum*); 15400, 1 dry; E23744, 1 dry. **VIRGIN ISLANDS:** USNM cat. no. 15391, 1 dry (lot originally included 2 *O. isocanthum*). **BELIZE:** LACM cat. nos. 80-155.1, 5 alc; 80-156.1, 1 alc; 80-157.1, 1 alc; 81-222.1, 4 alc; 81-223.1, 4 alc; 81-224.1, 2 alc; 81-225.1, 1 alc; 81-226.1, 2 alc; 81-227.1, 1 alc; 81-228.1, 2 alc; 81-230.1, 7 alc; 81-231.1, 3 alc; 81-232.1, 1 alc; 81-233.1, 1 alc; 81-234.1, 1 alc; 81-235.1, 1 alc; 81-236.1, 1 alc; 82-124.1, 3 alc; 83-214.1, 4 alc; 83-220.1, 2 alc; 83-221.1, 1 alc; 85-455.1, 3 alc; 85-164.3, 1 alc; 85-458.1, 2 alc; 86-56.1, 1 alc; USNM cat. nos. E17688, 1 dry; E19913, 1 alc; E19916, 1 alc; E21164, 2 alc; E21240, 3 alc; E21253, 2 alc; E21261, 1 alc; E30601, 1 alc.

DIAGNOSIS. Arms 6 in number. Disk covered with short tubercles, gradually increasing in size toward radial shields. Dorsal scales bumpy, appearing fused together. Primary plates absent. Three oral papillae, distalmost pair thick, operculate, clos-

ing part of oral slit. Three arm spines, tapering to narrow tips; middle spine curved, swollen at base, drastically narrowed near midshaft, excavated distally. Radial shields nearly bare of tubercles, narrow; thick, bead-shaped ossicles joined to distal margin. Adoral shields with distal lobes separated by first ventral arm plates. Proximal dorsal arm plates rounded triangular, slightly wider than long, separated nearly entire length of arm. Lateral arm plate stereom with expanded peripheral trabeculae. Ventral arm plate length exceeds width.

DESCRIPTION OF HOLOTYPE. Disk diameter 4.4 mm; longest arm 18 mm, regenerating. Disk hexagonal in outline, indented interradially, flattened dorsally, inflated near arms, bearing short blunt spines above and below. Arm joints below disk narrower than those beyond edge of disk. Arms slender, tapering, dorsoventrally flattened only near tip; joints set off by constrictions of lateral arm plates. Major ossicles of the disk and arms are thickened, dorsal arm plates more markedly so than ventral arm plates.

Body wall pliable, bumpy, scale covered. Scale edges not discernable; swollen central region on many scales bearing blunt tubercles. Most tubercles 0.04–0.2 mm tall, size gradually increasing toward edge of disk near radial shield; small tubercles broader at base than tip, larger tubercles not tapering. Radial shields clearly visible, bearing very few tiny spines; diverging and broader proximally, length approximately one-quarter diameter of disk. Thick, bead-shaped plate borne on narrow distal end of radial shield.

Infradental papillae paired, blocklike, in contact; middle oral papillae slightly larger than infradental, pyramidal, broad edge facing oral slit; distal oral papilla largest, spanning middle papilla to first ventral arm plate, quadrilateral, much longer than wide, elongate inner edge deeply incised and ridged. Distalmost papillae of adjacent jaws in contact, sealing outer oral gap. Teeth chisel-shaped, narrowing proximally such that tips of adjacent teeth not in contact; proximal edge straight, stereom imperforate.

Oral shields small, arrowhead-shaped, length nearly equal to width, approximately equal in size to an adoral shield, with sharply pointed proximal apex, proximal edges somewhat concave, lateral edges short, distal edge bluntly rounded. Shield depressed at center. Madreporite of similar shape, slightly larger.

Adoral shield gently curving, quadrilateral, with part of convex adradial edge adjoining incurved side of oral shield, concave radial edge facing mouth. Adoral shields with inner ends meeting broadly proximal to oral shield, outer ends separated by first ventral arm plate.

Prominent, swollen genital scale bridging oral shield and genital slit; row of thin, smooth scales sharply delineates edge of slit. Bursal slit narrow, spanning approximately $\frac{2}{3}$ length of interradius; slit inconspicuous, obscured by arm.

Dorsal arm plates rounded-triangular, slightly wider than long; apex rounded, lateral edges convex, distal edge nearly straight, with medial bulge raised above proximal surface of following plate. Proximal plates nearly touching, most separated by lateral arm plates, gap increasing distally.

Lateral arm plates with stereom of expanded peripheral trabeculae appearing as transparent, microscopic grains. Lateral plates constricted proximally, distal end broadened, forming thick spine-bearing ridge.

Three arm spines, erect, with rounded base, somewhat dorsoventrally flattened, gradually tapering to blunt tip. Dorsal spine longest, length less than dorsal arm plate. Middle spine appearing curved: bulging at base, much narrower near midshaft, more excavated distally.

First ventral arm plate, small, pentagonal, straight-sided, inserted at distal edge of jaw slit, adjoined laterally by adoral shields. Other ventral arm plates pentagonal, proximal edges meeting at rounded apex, lateral edges concave, distal edge convex, thickened. Length of second ventral arm plate equals width, distal plates longer than wide. First several ventral arm plates beyond edge of disk overlapping other plates nearly in contact.

Tentacle scales paired, flattened, spinelike with blunt tip, only partially covering tentacle pore; proximal scale on lateral arm plate slightly smaller than more distal scale on ventral arm plate.

Coloration. In alcohol yellowish, arm spines and tips of radial shields white. Arms banded with pale brown pattern on the dorsal arms plates. In life, specimens typically have a pale disk, mottled with rust-colored patches; the arms are tan with irregular rusty marks and gray-brown blotches forming a median chainlike pattern, the arm spines are pale and may have reddish orange tips.

VARIATIONS. Specimens examined have disk diameters from 1.0 to 4.4 mm and arm lengths from 6.8 to 19 mm. Maximum disk diameter/arm length ratio is 1/7.4. The majority of individuals have 6 arms of nearly equal length, or 3 long arms and 3 short regenerating arms. Rarely, unmistakable specimens of *O. siva* possess 5 arms. Of the specimens examined, those with 5 arms were distributed as follows: none from localities between North Carolina and Georgia ($n = 5$), 1.8% (3 of 165) from Belize, 6.3% (3 of 47) from Looe Key, Florida, and 7.6% (2 of 26) from Florida Bay. Not even the smallest specimens examined have discernable primary plates. Some Belizean specimens have aberrant swollen joints in the central region of the arm.

COMPARISON. Four *Ophiostigma* species are now recognized, of which only *O. siva* is fissiparous. The latter is readily distinguished from the sympatric *O. isocanthum* by characteristics of its dorsal arm plates (separate rather than in contact), arm spines (abruptly narrowed rather than peglike), and adoral shields (separate rather than united in a ring). The disk lacks strikingly prominent tubercles near the radial shields that characterize its congener.

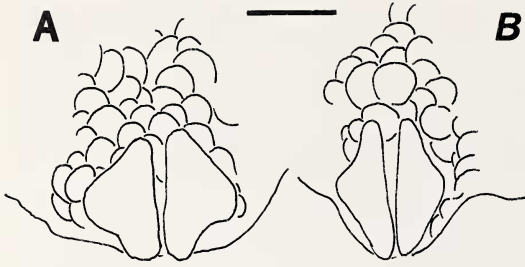


Figure 4. A portion of the inner surface of the disk wall, showing radial shields and surrounding scales of **A**, *Ophiostigma isocanthum* (Say), disk diameter = 2.8 mm (USNM E29141); **B**, *Ophiostigma siva*, new species, disk diameter = 2.8 mm (LACM 83-219.1). Scale bar = 0.5 mm.

Furthermore, by dissecting open the disks of both species, a marked difference can be seen in the shapes of the radial shields (Fig. 4A, B).

Ophiostigma abnorme (Lyman, 1878) is unique within the genus in having clearly demarcated, imbricating disk scales. Unlike *O. isocanthum* it has relatively few disk tubercles, which are spinelike, adoral shields not in contact distally, and narrow radial shields 3 times longer than wide (Madsen, 1970). Differences between *Ophiostigma tenue* Lütken, 1856, and *O. isocanthum* include the shape of oral and adoral shields and the pattern of disk granules (Koehler, 1913; Nielsen, 1932). *Ophiostigma rugosum* H.L. Clark, 1918, is distinguished by the disk covering composed of widely spaced tubercles and radial shields free of tubercles but with edges concealed by a thick integument. Its lateral arm plates, described as meeting above and below except at the base of the arm, also set it apart. *Ophiostigma formosa* Lütken, 1856, has been transferred to *Dougaloplus* (A.M. Clark, 1970).

Ophiostigma abnorme is distributed from the Gulf of Mexico (in deep water), to Ascension Island, Cape Verde Islands, the Gulf of Guinea, and Gold Coast of Africa, from 16 to 185 m (Madsen, 1970). *O. tenue* is known from the Pacific coasts of Nicaragua and Panama, from 7 to 46 m (Lütken, 1859; Nielsen, 1932). *O. rugosum* is reported from the Philippines (H.L. Clark, 1918).

DISTRIBUTION. Reliable records in the literature (noted in the synonymy) include Bermuda, the Florida Keys and Tortugas, Puerto Rico, Jamaica, St. Thomas, and Belize, from less than 1 m to 42 m. Material in USNM and LACM collections shows that the species also occurs off North Carolina and South Carolina and in the Gulf of Mexico, at depths to 99 m. *O. siva* may have been collected at other localities and identified as *O. isocanthum* by previous authors.

BIOLOGY. This species is fissiparous, as suggested by H.L. Clark (1901, 1942) and Hotchkiss (1982). The hundreds of specimens examined typically have 3 longer and 3 shorter arms, and every

stage between recent disk division and nearly complete arm regeneration is in evidence. The incidence of 5-armed individuals is very low, as noted under Variations. Among the specimens examined, there was no evidence of a development or transformation of 6-armed to 5-armed individuals. A small number of specimens that were dissected lacked discernable gonads, and swelling of the body wall (indicative of ripe gonads) was not observed in any specimens examined. This may indicate that sexual reproduction of the species, if it occurs, is uncommon.

It is notable that both *O. isocanthum* and *O. siva* can occur in the same localities and habitats and sometimes in the same clump of substrate (Hendler et al., 1995). *O. siva* ranges from the back reef to forereef slope zones and is most abundant in calcareous algae, such as the *Halimeda opuntia* (Hendler and Littman, 1986; Hendler and Peck, 1988).

Relative numbers of *O. isocanthum* and *O. siva* vary widely among the available collections. Among 350 individuals of *Ophiostigma* from North Carolina to Georgia, from 20- to 30-m depths, only 1.4% were *O. siva*. In contrast, 69% of the individuals from Looe Key and Florida Bay, Florida, and from Belize, all from less than 24 m, were *O. siva*. Factors related to latitude may affect abundance of the 2 species, and in a circumscribed region other environmental factors may prevail. For example, in Belize, *O. isocanthum* predominated in collections from mangrove cays, and *O. siva* was by far more abundant in the reef habitat, but exactly comparable, quantitative collections were not made in the 2 habitats.

As noted for *O. isocanthum*, individuals are collected with particles of sediment stuck to the disk and arms, and the particles continue to adhere to preserved specimens. Evidently, these animals produce a mucus that binds sediment to the body wall.

Genus *Amphioplus* Verrill, 1899

Subgenus *Amphioplus* Verrill (as restricted, A.M. Clark, 1970)

Amphioplus (*Amphioplus*) *sepultus*, new species

Figures 5A–C, 6D–I

Amphioplus abdita: Koehler, 1914:71 (not *Amphipholis* [= *Amphioplus*] *abdita* Verrill, 1871, in part).

Amphioplus abditus H.L. Clark, 1918:294 (not Verrill, 1871); 1919:56, 59, 60, 66 (not Verrill, 1871, in part); 1933:38, 55–56, 141 (not Verrill, 1871, in part). A.H. Clark, 1921:42 (not Verrill, 1871); 1954:377 (not Verrill, 1871). Mortensen, 1933:110, 111 (not Verrill, 1871, in part). Pearson, 1937:70 (not Verrill, 1871). McNulty, 1961: 411, 414, 418, 422, 424, 429–431 (not Verrill, 1871); 1970:36, 40–43, 46, 49, 51, 54, 57, 59 (not Verrill, 1871). Tabb and Manning, 1961:566 (not

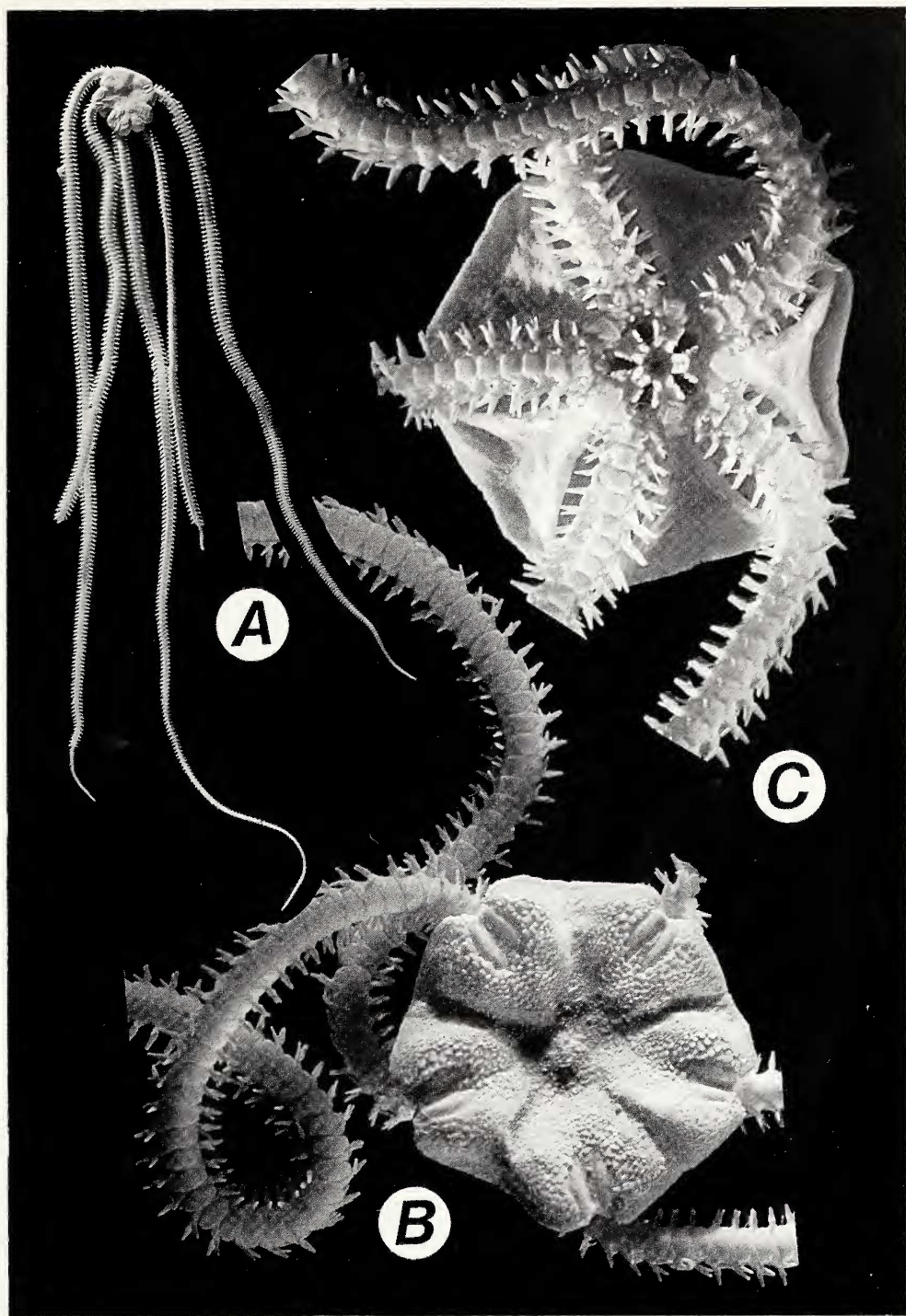


Figure 5. *Amphipolus sepultus*, new species: A, paratype LACM 85-363.4, entire, dorsal view, disk diameter = 7.0 mm, longest arm = 90 mm; B, holotype (USNM E14025), disk, dorsal view; C, disk, ventral view. Disk diameter = 8.7 mm.

Verrill, 1871). McNulty et al., 1962a:218, 223, 224, 229 (not Verrill, 1871). McNulty et al., 1962b:329 (not Verrill, 1871). Thomas, 1962:636, 651-654, 656, 657, 660 (not Verrill, 1871, in

part). Parslow and A.M. Clark, 1963:26, table I (not Verrill, 1871). O'Gower and Wacasey, 1967: 197 (not Verrill, 1871). Halpern, 1970:630 (not Verrill, 1871). Hudson et al., 1970:9 (not Verrill,

1871). A.M. Clark, 1970:48, 56 (not Verrill, 1871, in part). Singletary, 1971:940 (not Verrill, 1871). Woodley, 1975:29, 37, 44 (not Verrill, 1871). *Amphioplus sepultus*: Hendler, 1973 (*nomen nudum*):i-255; 1991 (*nomen nudum*):366, 377, 384, 402, 412, 414, 421, 424. Pettibone, 1993 (*nomen nudum*):41, 42. *Amphioplus* sp. Humes and Hendler, 1972:539, 541, 546, 551, 555.

The taxonomic status of the new species and two congeners, *Amphioplus abditus* (Verrill, 1871) and *Amphioplus macilentus* (Verrill, 1882), has been chronically confused. The latter two species have been lumped and split several times, and the new species has, with few exceptions, gone unrecognized (Hendler, 1973, 1991; Pettibone, 1993). However, distinctions among the three taxa are clearcut, based on external and internal morphology, ontogeny, and physiology (Hendler, 1973).

A. abditus was originally described from Connecticut, off New Haven (Verrill, 1871). Its confirmed range extends from Grand Manan, Maine, to Sapelo Island, Georgia, typically in shallow water but at depths to 40 m (Hendler, 1973). *Amphioplus macilentus* was first discovered off Martha's Vineyard, Massachusetts and ranges at least to North Carolina on the edge of the continental shelf between 97 and 210 m (Verrill, 1885).

Koehler (1914) was the first to record the new species from Florida but, as reflected in the synonymy above, he and other authors identified the Floridian specimens as *A. abditus*. Under the name *A. abditus*, Thomas (1962:654) considered *A. sepultus* "the most common intertidal amphiuroid of South Florida."

ETYMOLOGY. *Sepultus*, the masculine form of the Latin participle for "buried," in reference to the burrowing habit of the species.

MATERIAL EXAMINED. Designated types originally cataloged as *A. abditus* unless otherwise noted.

Holotype. FLORIDA, ATLANTIC: (USNM E14025), alc, 9 Jan. 1972, Virginia Key, Miami, Florida, 1.5 m, coll. G. Hendler.

Paratypes. FLORIDA, ATLANTIC: (LACM 68-456.1), 1+ alc, Sta. 15-68, 27 Mar. 1968, Biscayne Bay, Miami, Florida, coll. R.L. Singletary and T. Borkowski; (LACM 85-265.4), originally as *Amphioplus* sp., 1 alc, Sta. LK 45, 15 May 1985, 24°33.7'N, 81°25.7'W, Looe Key National Marine Sanctuary, Florida Keys, Florida, 11 m, Hendler et al.; (LACM 88-195.2), originally as *A. sepultus*, 7 alc, Sta. MI-I/88-2, 17 Jan. 1988, 25°44'N, 80°10'W, Seaquarium flats, Rickenbacker Causeway, Virginia Key, Biscayne Bay, Miami, Florida, 0-1 m, coll. J.E. Miller; (LACM 88-196.2), originally as *A. sepultus*, 1 alc, Sta. MI-I/88-3, 17 Jan. 1988, 25°43.5'N, 80°09.5'W, NW Point, Key Biscayne, Florida, 0-1 m, J.E. Miller et al.; (LACM 88-196.3), originally as *A. sepultus*, 1 alc, Sta. MI-I/88-3, 17 Jan. 1988, 25°43'N, 80°09.5'W, NW Point, Key Biscayne, Florida, 0-1 m, coll. J.E. Miller; (USNM E14026), 29 alc, 9 Jan. 1972, Virginia Key, Miami, Florida, 1.5 m, coll. G. Hendler; SOUTHWEST FLORIDA, GULF OF MEXICO: (LACM 85-361.1), originally as *A. sepultus*, 2 alc,

Sta. FK-04, 11 May 1985, 24°41'N, 81°13.5'W, W end of Seven Mile Bridge, E end of Little Duck Key, 1 m, coll. G. Hendler et al.; (LACM 85-362.2), originally as *A. sepultus*, 5 alc, Sta. LK 05, 11 May 1985, 24°39.1'N, 81°18'W, E end of W Summerland Key, 0.3-0.9 m, coll. G. Hendler et al.; (LACM 85-363.4), originally as *A. sepultus*, 5 alc, Sta. FK-06, 11 May 1985, 24°42'N, 81°24.7'W, N end of Middle Torch Key, Florida, coll. G. Hendler et al.

Other Material Examined. FLORIDA: cat. no. MCZ 6747, 1 dry. FLORIDA, ATLANTIC: MCZ cat. nos. 1457, 1 dry; 1533, 1 alc; 5505, 34 alc; 5506, 39 dry; 5571, 1 dry; uncat. lot, several. SOUTHWEST FLORIDA, GULF OF MEXICO: USNM cat. nos. 6866, 3+ alc; 12674, 50+ alc; 14002, 1 alc; 33873, 1 dry; 38924, 5 dry; MCZ cat. nos. 1458, 1 dry; 4055, 2 dry; 4056, 2 alc; 4239, 4 dry; 4240, 2 dry; 4282, 4 alc; 4283, 3 alc; 6647, 2 dry; 6660, 2 dry; UML cat. nos. 41.99, 1 alc; 41.101, 14 alc; 41.136, 2 alc.

DIAGNOSIS. Entire disk covered with fine, imbricating scales; scales largest and thickest near radial shields and disk edge. Radial shields 2-3 times longer than wide, separated by scales except distally. Five oral papillae. Oral shields twice as long as wide, spearhead-shaped, with small, paired lateral lobes. Two tentacle scales. Three arm spines; dorsal shortest, laterally compressed, tapering, tip rounded; middle spine broadest, dorsoventrally flattened, tapering to blunt flat tip; ventral spine as long as middle spine, curving ventrodistally, with deep channel on dorsal-distal surface. Microscopic spinules most prominent on middle spine.

DESCRIPTION OF HOLOTYPE. Disk diameter 8.7 mm; arms broken, approximately 11 cm in length. Disk thin, flexible, rounded pentagonal, outpouching between arms, but indented interradially. Arms slender, narrowed near disk, distalmost third of arm tapering to filiform tip. Arms gently rounded dorsally, flattened ventrally; dorsal arm plates of successive joints in contact, successive ventral arm plates slightly separated by lateral arm plates, lateral arm plates bridged by soft tissue.

Disk entirely covered with small, imbricating scales; scales smallest at center of disk, largest around radial shields; enlarged scales at disk edge demarcate dorsal and lateral disk surfaces. Primary plates minute, widely separated. Radial shields with straight adradial edge, broadly rounded abradial edge, thickened medial ridge, thick distal tip directed adradially; shields tapering proximally, 2-3 times longer than wide; separated by wedge of scales proximally, joined distally.

Each jaw bears 5 pairs of oral papillae; infradental largest, separated, thick, blocklike, longest axis dorsoventral; buccal tentacle scale smallest, blunt spine-shaped, high in jaw; 2 flattened scales on oral plate, proximal scale smaller, distal scale larger, triangular to quadrangular; outermost scale seated between adoral shield and first ventral arm plate. Teeth with concave tips, stereom of proximal edge imperforate.

Oral shield narrow, blunt spearhead-shaped with small lateral lobes, approximately 1.5 times as long as wide. Madreporite slightly larger than shields,

asymmetrical. Adoral shield 3-lobed; largest lobes of adjacent adoral plates meet proximally to oral plate; small radial lobe in contact with first ventral arm plate; thin adradial lobe touching bursal slit.

Bursal slits spacious, extending to disk edge. Ventral interbranchial field covered by fine, flakelike, imbricating scales; scale size greatest near bursal slit; density of scales diminishing near oral shield.

Dorsal arm plates ovoidal hexagonal, 1.5–1.8 times broader than long; proximolateral edges slightly concave; short lateral edges truncate; distal edge broad, convex. Plates touching or nearly in contact, distal edge contacting or overlapping proximal edge of adjacent plate.

Lateral arm plates narrow in dorsal aspect, with prominent spine-bearing ridge conspicuously protruding from arm. Three arm spines, with broad bases, tapering, equal in length to arm joint; dorsal spine shortest, laterally compressed, tip rounded, channel on lateral surface (Fig. 6D, G); middle spine broadest, dorsoventrally flattened, with blunt, flat tip, with channels on dorsal and ventral edges (Fig. 6E, H); ventral spine as long as middle spine, flattened dorsally, convex ventrally, curving ventro-posteriorly, with deep channel on dorsal-distal surface (Fig. 6F, I). All spines with microscopic spinules, rugosity most prominent on middle spine.

Ventral arm plates pentagonal, edges slightly concave, barely separated by lateral arm plates, proximolateral edges shortest, distal edge longest. Second plate longer than broad, center depressed, lateral and distal edges raised; plate width increasing to fifth or sixth plate, width/length ratio 0.9/1.1. Plates touching or nearly in contact.

Two tentacle scales proximally, in contact, reduced to 1 scale near arm tip; larger scale arising on lateral and ventral arm plates, smaller scale on ventral arm plate. Tube foot with smooth shaft and bulbous tip.

Coloration. In life, pigmentation variable; gray or brown overall, variegated with light gray or reddish tan and contrasting dark gray. Arms dorsally mottled, sometimes having pale middorsal line. Spines pale with dark basal spot internally. Disk coloration uniform to the naked eye, at low magnification appearing speckled, darker scales having a pale border. Radial shield contrastingly dark or mottled, with pale edges and distal tip. Ventral disk scales light gray to tan. First ventral arm plate and infradental papillae densely pigmented. Adoral and genital shields often patterned with black. Ventral arm plates darkest proximally, blotched distally; sometimes with a midventral stripe. Color of testes whitish. Ovaries off-white to gray, sometimes with yellow or green tinge. In alcohol color fades to white.

VARIATIONS. Disk diameters of specimens examined range from 0.3 to 0.9 cm, with arm lengths from 3 to 11 cm. The distalmost (accessory) oral papillae may number more than 1 in large individuals. As individuals grow, the primary plates become more widely separated from one another, and

the central and radial plates display negative allometry in diameter. The numbers of tentacle scales range from 0 to 5 on the proximal arm joints. The oral shields vary in shape, sometimes subelliptical, pentagonal, or hexagonal, sometimes with the proximal edge squared off. The madreporite usually has 1 perforation, occasionally up to 4. Proximal corners of the adoral shields may be touching or separate and may be concealed by the proximal edge of the oral shield. Individuals from reef environments tend to be smaller and more pale than those from eutrophic Gulf Coast habitats.

Details of internal anatomy, including oral plate shape, have been documented (Hendler, 1973). In the place of peristomial plates there are groups of small thin scales. Arm vertebrae are perforate. Wedge-shaped dental plates possess up to 8, rarely 9, foramina. In ripe individuals, oocytes number 3,000–9,000, with a mean diameter of 0.17 mm.

COMPARISONS. *A. (Amphioplus) sepultus* differs from the more than 30 species in the nominotypical subgenus in having 3 blunt arm spines with the morphology noted above. The characteristic middle arm spine is similar in shape to those in *A. platyacanthus* (Murakami, 1943), but the latter species has 4 arm spines.

Amphioplus sepultus is readily distinguished from its Floridian congeners. *A. thrombodes* H.L. Clark, 1918, differs in having papillose scales on the dorsal surface of the disk and only 1 tentacle scale. *A. coniotodes* H.L. Clark, 1918, differs in having the disk extremely fine-scaled dorsally and naked ventrally, with thin radial shields that are 4 times longer than wide, and very elongate arms, 20 times the disk diameter in length.

The distinctions between *A. sepultus*, its larger northern congener *A. abditus*, and its smaller deep-water congener *A. macilentus*, have been described at length (Hendler, 1973). Distinguishing features include the structure of the ventral arm plates and oral plates and are most readily apparent for the arm spines.

Individuals of the 3 species of equivalent size have arm spines of contrasting length (Hendler, 1973) and shape. The 3 arm spines of *A. macilentus* are all slender and acutely pointed (Fig. 6A–C). The dorsal and ventral spines of *A. abditus* and *A. sepultus* are similarly shaped (e.g. Fig. 6G, I, M, O); however, the middle spine of *A. abditus* is constricted, with an expanded tip bearing large spinules (Fig. 6K, N, Q), contrasting with the tapering, blunt-tipped spine of *A. sepultus* (Fig. 6E, H).

DISTRIBUTION. Florida waters, from Biscayne Bay to the Dry Tortugas on the Atlantic Coast, and from Flamingo in Florida Bay to Destin on the Gulf of Mexico coast; intertidal to 82-m depth.

BIOLOGY. *A. sepultus* is a burrowing deposit feeder, ingesting sediment and plant material, algae, pollen, fecal pellets, and microscopic invertebrates (Hendler, 1973). Its arms undulate beneath the sediment, circulating water through the burrow; a “respiratory fringe” of mucus and sediment on the arm



Figure 6. Light microscope preparations showing arm spine morphologies of *Amphioplus macilentus* (Verrill), *A. sepultus*, new species, and *A. abditus* (Verrill); differences related to body size are illustrated for the latter two species. *A. macilentus*: disk diameter = 2.3–4.2 mm—A, dorsal spine; B, middle spine; C, ventral spine. *A. sepultus*: disk diameter = 2.4–4.4 mm—D, dorsal spine; E, middle spine; F, ventral spine; disk diameter = 4.4–6.4 mm—G, dorsal spine; H, middle spine; I, ventral spine. *A. abditus*: disk diameter = 3.5–4.9 mm—J, dorsal spine; K, middle spine; L, ventral spine; disk diameter = 5.2–9.4 mm—M, dorsal spine; N, middle spine; O, ventral spine; disk diameter = 14.4–15.3 mm—P, dorsal spine; Q, middle spine; R, ventral spine. Scale bar = 0.5 mm.

spines creates a gasket between the arm and the burrow wall (Woodley, 1975).

Amphioplus sepultus (as *A. abditus*) has been designated a dominant in an “*Amphioplus*-*Dosinia* community,” where there may be several hundred individuals per square meter (McNulty et al., 1962a, b), and has been found to occupy other benthic communities (McNulty, 1970). The species has been recorded from soft sticky sediment (Pearson, 1937), carbonate mud (Hudson et al., 1970), and firm sandy mud (H.L. Clark, 1918) and often associated with marine spermatophytes (Pearson, 1937; McNulty, 1961; O’Gower and Wacasey, 1967) and sometimes near sewage pollution (McNulty, 1961).

Halpern (1970) noted that this species is a food item of the sea star *Luidia senegalensis* (Lamarck), and Singletary (1971) determined its upper lethal temperature limit, approximately 40°C. The annual reproductive, feeding, respiratory, and growth cycles of the species have been examined (Hendler, 1973). Two external copepod associates have been reported from *A. sepultus* (Humes and Hendler, 1972); an internal copepod and nauplii (which castrates the host) live in the coelom, a metacercaria (Subfamily Allocreadioidea) occurs in the gonad, a sessile rotifer (unidentified) lives on the arm spines, and a polynoid polychaete (*Malmgreniella macrariae* Pettibone) and a bivalve (*Montacuta* sp.) are found on the disk (Hendler, 1973; Pettibone, 1993).

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